

Using reproductive value to estimate key parameters in density-independent age-structured populations

Steinar Engen^{a,*}, Russell Lande^{b,*}, Bernt-Erik Sæther^c, Marco Festa-Bianchet^d

^aDepartment of Mathematical Sciences, Norwegian University of Science and Technology, N-7491 Trondheim, Norway

^bDepartment of Biology 0116, University of California - San Diego, La Jolla CA 92093, USA

^cDepartment of Biology, Norwegian University of Science and Technology, N-7491 Trondheim, Norway

^dDépartement de Biologie, Université de Sherbrooke, Qec., Canada J1K 2R1

Received 15 May 2006; accepted 2 August 2006

Available online 14 August 2006

Abstract

The dynamics of reproductive value are used to provide a simple derivation of Tuljapurkar's approximation for the long-run growth rate and environmental variance of $\ln N$, in a density-independent age-structured population in a random environment. With no environmental autocorrelation, the dynamics of total population size, N , generally shows time lags and autocorrelation caused by life history, which may strongly bias estimates of environmental variance obtained by ignoring age structure. In contrast, the total reproductive value, V , is Markovian and obeys a first-order autoregressive process. This suggests a simple method for estimating the environmental variance, and avoiding potentially large bias due to age-structure fluctuations, by converting a multivariate time series of age structure to a univariate time series of $\ln V$. We illustrate the method by estimating the long-run growth rate and the environmental variance in an exponentially growing population of Bighorn Sheep.

© 2006 Elsevier Ltd. All rights reserved.

Keywords: Age structure; Environmental variance; Reproductive value; Demographic variance; Bighorn Sheep

1. Introduction

Demographic and environmental stochasticity create continual fluctuations in population size and age structure, augmented by time lags in the life history and density dependence (Coulson et al., 2001; Clutton-Brock and Coulson, 2002; Lande et al., 2002a,b). The interaction of these processes makes it difficult to separate their effects on population dynamics. For density-independent populations, three key parameters are the long-run growth rate, the environmental variance (Cohen, 1977; Tuljapurkar, 1982) and the demographic variance (Engen et al., 2005). We use the dynamics of reproductive value to derive a simplified description of a density-independent age-structured

population as a one-dimensional Markovian process based on these parameters, which facilitates their estimation from population data.

Environmental stochasticity affects the age-specific vital rates of all individuals in a population in the same or similar way, producing a constant variance among years in population growth rate, σ_e^2 , independent of population size. In contrast, demographic stochasticity is caused by variation in fitness among individuals within years, usually attributed to independent chance events of individual survival and reproduction, producing random changes in population growth rate, with a variance inversely proportional to population size, σ_d^2/N . Thus, environmental stochasticity dominates for population sizes greater than the ratio of the demographic and environmental variances, $N > \sigma_d^2/\sigma_e^2$ (Lande et al., 2003).

For a large age-structured population with no density regulation, in an environment where the age-specific vital rates fluctuate with a stationary distribution, Cohen (1977)

*Corresponding authors. Tel.: +47 7359 1747; fax: +47 7359 3524.

E-mail addresses: steinaen@math.ntnu.no (S. Engen), rlande@ucsd.edu (R. Lande), Bernt-Erik.Sather@bio.ntnu.no (B.-E. Sæther), marco.festa-bianchet@usherbrooke.ca (M. Festa-Bianchet).

defined the long-run growth rate as the asymptotic rate of increase of the natural log of total population size. The long-run growth rate, and its environmental variance, are of fundamental importance for stochastic dynamics of age-structured populations because starting from a given total size all population trajectories grow asymptotically at the same rate.

Tuljapurkar (1982) derived an approximate expression for the long-run growth rate assuming small environmental stochasticity. This approximation has been shown to be quite accurate for a large range of parameter-values (Lande et al., 2003). Lande and Orzack (1988) showed that the long-run growth rate, the environmental variance and the initial total reproductive value are key parameters that can be used to accurately reduce the asymptotic behavior and (quasi-)extinction dynamics of a density-independent age-structured population to a one-dimensional diffusion process.

Engen et al. (2005) extended this approach to include the net demographic stochasticity in the life history described by the demographic variance. Analysis of this basic model shows that age structure generates covariances between environmental noise terms at time lags of the order of a generation, which has also been found in density-dependent models (Lande et al., 2002a,b). Although the diffusion approximation does not include these time lags, which produce transient fluctuations and even oscillations, it still gives the correct distribution of future population sizes over long times because the transient fluctuations due to age-structure are damped within a few generations as the population fluctuates around a stable or average age distribution.

Reliable projections of age-structured populations require that the demographic and environmental variances can be estimated from data. The demographic variance can be estimated simply and accurately from individual data on reproduction and survival (Engen et al., 2005). In models without age structure the environmental variance is usually estimated from time series observations of the total population size correcting for demographic stochasticity (Sæther et al., 1998). In age-structured populations, however, the estimation of σ_c^2 is more difficult due to time lags and transient fluctuations generated by life history. If the long-run growth rate and the environmental variance are estimated as in populations without age structure (Dennis et al., 1991; Holmes, 2001; Morris and Doak, 2002; Lande et al., 2003) transient fluctuations caused by age-structure may severely bias estimates of the environmental variance.

Here we show for density-independent populations how this bias in estimating the environmental variance can be avoided simply by working with the total reproductive value of the population rather than the population size. If the environmental variables affecting the fluctuations can be described as a white noise process (with no temporal autocorrelation), the dynamics of reproductive value will also, to the first order, be a process

with white noise. Hence the stochastic dynamics of the total reproductive value can be analyzed as a process without age-structure. For large population sizes, the residual variation (the difference between the log of reproductive value and the log of population size) is a stationary autocorrelated process with mean zero which we also analyze. Tuljapurkar and Lee (1997) also analyzed the dynamics of reproductive value in a density-independent population, but did not apply their results to the derivation or estimation of the long-run growth rate and the environmental variance. Lande et al. (2006) extend the application of reproductive value to density-dependent populations.

In this paper we emphasize the large bias in estimates of environmental variance that can arise in previous methods for analyzing univariate population time series that do not account for age-structure fluctuations. We apply our method to a population of Bighorn Sheep *Ovis canadensis* in western Canada during a period of density-independent growth by estimating the long-run growth rate and the environmental variance using time series data on fluctuations in the age structure.

2. Dynamics of reproductive value

Denoting the transpose of a vector or matrix by $'$ we write $\mathbf{n} = (n_1, \dots, n_k)'$ for the column vector describing a population with k age or stage classes censused just before reproduction (Caswell, 1989, 2001). The population vector in year $t + 1$ is given by $\mathbf{n}_{t+1} = \mathbf{M}_t \mathbf{n}_t$ where the subscript t denotes time when required, and \mathbf{M}_t is a stochastic projection matrix operating on the population in year t . This matrix fluctuates between years, the components being the mean of realized individual vital rates. We assume no density regulation, and initially no demographic stochasticity, so that the distribution of \mathbf{M}_t is independent of time. We write $\mathbf{M}_t = \mathbf{L} + \boldsymbol{\varepsilon}_t$, where \mathbf{L} is the expectation of \mathbf{M}_t , and $\boldsymbol{\varepsilon}_t$ denotes the stochastic deviation from the expected value so that $E\boldsymbol{\varepsilon}_t = \mathbf{0}$, in accordance with Tuljapurkar (1982).

Let λ denote the dominant (or leading) eigenvalue of \mathbf{L} (with largest modulus) with corresponding right (column) eigenvector $\mathbf{u} = (u_1, \dots, u_k)'$ and left (row) eigenvector $\mathbf{v} = (v_1, \dots, v_k)$, so that $\mathbf{L}\mathbf{u} = \lambda\mathbf{u}$ and $\mathbf{v}\mathbf{L} = \lambda\mathbf{v}$. Scaling \mathbf{u} such that the sum of the components is 1, \mathbf{u} is the stable age distribution in the corresponding deterministic model. If \mathbf{v} is scaled so that $\mathbf{v}\mathbf{u} = 1$ then the components of \mathbf{v} are the reproductive values for the different age-classes. The size of the total population, say N_t , will then after some time in a constant environment grow approximately exponentially at a rate proportional to the initial total reproductive value in the population, $N_t \approx \lambda^t \mathbf{v}\mathbf{n}_0$ (Charlesworth, 1994; Caswell, 2001; Lande et al., 2003).

The total reproductive value at time t is $V_t = \mathbf{v}\mathbf{n}_t$. If there is no density regulation then in a stochastic environment the expected value of this quantity will grow exactly

exponentially since

$$E[V_{t+1}|V_t] = \mathbf{v}\mathbf{L}\mathbf{n}_t = \lambda\mathbf{v}\mathbf{n}_t = \lambda V_t \tag{1}$$

without any transient fluctuations in the initial phase even if the population structure starts far from the stable age distribution (Fisher, 1958; Caswell, 2001, p. 93; Lande et al., 2003, p. 57).

Eq. (1) indicates that stochastic dynamics also may be simpler to describe if we work with V_t rather than N_t . The autocorrelations found in time series of age-structured populations are often mainly due to transient fluctuations around the exponential growth curve generated by deviations from the stable age distribution (Lande et al., 2002a). Since the process V_t does not show these transient fluctuations caused by age structure, we should expect the stochastic dynamics of the reproductive value, given by $V_{t+1} = \mathbf{v}(\mathbf{L} + \boldsymbol{\varepsilon}_t)\mathbf{n}_t = \lambda V_t + \mathbf{v}\boldsymbol{\varepsilon}_t\mathbf{n}_t$, to be simpler than that of N_t . If we ignore second-order terms by approximating \mathbf{n}_t in the stochastic term by a vector proportional to the stable age distribution, say $\mathbf{n}_t \approx c_t\mathbf{u}$ and with the same total reproductive value $V_t = \mathbf{v}c_t\mathbf{u}$ we must require that $c_t = V_t$ since $\mathbf{v}\mathbf{u} = 1$, giving

$$V_{t+1} = \lambda V_t(1 + \lambda^{-1}\mathbf{v}\boldsymbol{\varepsilon}_t\mathbf{u}), \tag{2}$$

and $\text{Var}[V_{t+1}|V_t] \approx V_t^2 \text{Var}[\mathbf{v}\boldsymbol{\varepsilon}_t\mathbf{u}] = V_t^2\sigma_V^2$. Since $\partial\lambda/\partial L_{ij} = v_i u_j$ (Caswell, 1978, 2001, p. 209) this term can alternatively be written as

$$\sigma_V^2 = \sum_{ij} \sum_{kl} \frac{\partial\lambda}{\partial L_{ij}} \frac{\partial\lambda}{\partial L_{kl}} \text{Cov}[M_{ij}, M_{kl}]. \tag{3}$$

The long-run growth rate for the reproductive value, that is, the expected growth rate for the log of total reproductive value, is

$$s = E[\ln V_{t+1} - \ln V_t | \ln V_t] = r + E \ln(1 + \lambda^{-1}\mathbf{v}\boldsymbol{\varepsilon}_t\mathbf{u}),$$

where $r = \ln \lambda$ is the growth of the deterministic model defined by \mathbf{L} . Assuming that the stochastic term is small and using the second-order approximation for the logarithm we find $s \approx r - \frac{1}{2}\lambda^{-2} \text{Var}[\mathbf{v}\boldsymbol{\varepsilon}_t\mathbf{u}]$. Again using the relation $\partial\lambda/\partial L_{ij} = v_i u_j$ we obtain Tuljapurkar’s formula for the long-run growth rate and the environmental variance (Tuljapurkar, 1982)

$$s = r - \frac{1}{2}\sigma_e^2 \quad \text{and} \quad \sigma_e^2 = \lambda^{-2}\sigma_V^2. \tag{4a}$$

The process for the log reproductive value can be written as $\ln V_{t+1} = \ln V_t + s + \xi_t$,

where $\xi_t = \lambda^{-1}\mathbf{v}\boldsymbol{\varepsilon}_t\mathbf{u}$ so that $E\xi_t = 0$ and $\text{Var}[\xi_t] = \sigma_e^2$. To the first order, this process is Markovian, with no autocorrelation in the noise ξ_t if the stochastic projection matrices, \mathbf{M}_t , are independent between years. This explains why the long-run growth rate, s , is identical for $\ln N$ and $\ln V$ and why $\ln N$ can be accurately modeled as a diffusion process with infinitesimal mean s , infinitesimal variance σ_e^2 and initial value $\ln V_0$ (Lande and Orzack, 1988).

More generally, the log of any nonnegative linear combination of age classes must increase asymptotically

at rate s . This occurs because $V_t = \mathbf{v}\mathbf{n}_t$ is nonnegative (by the Perron–Frobenius theorem: Gantmacher, 1959; Caswell, 2001), hence \mathbf{v} must be a component of any nonnegative combination of age classes.

3. Fluctuations around the reproductive value

If the population has exactly the stable age-distribution of the deterministic model, then $\mathbf{n}_t/V_t = \mathbf{u}$. We shall study the fluctuations of the age-distribution by analyzing the deviation

$$\mathbf{x}_t = \mathbf{n}_t/V_t - \mathbf{u} = \frac{1}{V_t}(\mathbf{I} - \mathbf{u}\mathbf{v})\mathbf{n}_t, \tag{5}$$

where \mathbf{I} is the identity matrix. The quantity \mathbf{x}_t will fluctuate around zero as the age-structure fluctuates around the stable age-distribution. Writing $X_t = N_t/V_t - 1$ for the sum of the components of \mathbf{x}_t we find that $\ln N_t$ can be expressed as the sum of two processes

$$\ln N_t = \ln V_t + \ln(1 + X_t) \approx \ln V_t + X_t,$$

where the approximation is valid for small fluctuations in the age-structure. Hence, X_t is approximately the deviation between log population size and log of reproductive value.

We show in Appendix A that the multivariate process \mathbf{x}_t for small fluctuations in age structure is

$$\mathbf{x}_{t+1} = \mathbf{A}\mathbf{x}_t + \lambda^{-1}(\mathbf{I} - \mathbf{u}\mathbf{v})\boldsymbol{\varepsilon}_t\mathbf{u}, \tag{6}$$

where $\mathbf{A} = \lambda^{-1}\mathbf{L} - \mathbf{u}\mathbf{v}$.

Eqs. (5) and (6) reveal that the dynamics of \mathbf{x}_t resemble those for \mathbf{n}_t , after scaling and removing the component of environmental noise in the direction of the reproductive value vector \mathbf{v} . (This follows from the spectral form of a matrix with its eigenvectors obeying the orthogonality relationships $\mathbf{v}^{(i)}\mathbf{u}^{(j)} = 1$ if $i=j$ and 0 otherwise (Gantmacher, 1959).) The matrix $(\mathbf{I} - \mathbf{u}\mathbf{v})$ thus acts to filter the time series of the age distribution. The eigenvectors of \mathbf{A} are the same as those of \mathbf{L} with corresponding eigenvalues $0, \lambda_2/\lambda, \lambda_3/\lambda, \dots$. Thus, increasing powers of \mathbf{A} approach the zero matrix, so that assuming $\boldsymbol{\varepsilon}_t$ is a stationary process, the fluctuations in \mathbf{x}_t approach a stationary distribution. The root of largest modulus, λ_2/λ , describes the rate of approach to the stable age distribution in deterministic demography (Caswell, 1989, 2001).

Appendix A shows that the stationary distribution has mean $E\mathbf{x} = \mathbf{0}$ and covariance matrix

$$E[\mathbf{x}_t\mathbf{x}'_{t+\tau}] = \lambda^{-2} \sum_{p=1}^{\infty} \mathbf{G}_p\mathbf{S}\mathbf{G}'_{p+\tau}, \tag{7}$$

where the coefficients are $\mathbf{G}_p = \mathbf{A}^{p-1}(\mathbf{I} - \mathbf{u}\mathbf{v})$ with $\mathbf{A}^0 = \mathbf{I}$ and $\mathbf{S} = E[\boldsymbol{\varepsilon}\mathbf{u}\mathbf{u}'\boldsymbol{\varepsilon}']$ giving $S_{ij} = \sum_k \sum_l u_k u_l \text{Cov}[M_{ik}, M_{jl}]$. The covariance between X_t and $X_{t+\tau}$ is the sum of the components of $E[\mathbf{x}_t\mathbf{x}'_{t+\tau}]$. Appendix A also shows that the variance of the stationary distribution of X can be written as a sum of variances and covariances from components of the environmental noise in the directions of all the left

eigenvectors excluding the dominant eigenvector,

$$\sigma_X^2 = \sum_{i \geq 2} \sum_{j \geq 2} \frac{S^{(ij)}}{\lambda^2 - \lambda_i \lambda_j}, \tag{8}$$

where $S^{(ij)} = \mathbf{v}^{(i)} \mathbf{S} \mathbf{v}^{(j)}$ is the component of the environmental covariance between the i th and j th left eigenvectors.

4. Demographic stochasticity

For small population sizes demographic stochasticity has to be taken into account. This can be done by reinterpreting the covariances in Eq. (3), as in Engen et al. (2005). If \mathbf{z} is the vector of all environmental variables affecting the projection matrix \mathbf{M} , each covariance is split into a demographic and environmental component by conditioning on the environment, that is,

$$\text{Cov}[M_{ij}, M_{kl}] = \text{Cov}[E(M_{ij}|\mathbf{z}), E(M_{kl}|\mathbf{z})] + ECov[M_{ij}, M_{kl}|\mathbf{z}]. \tag{9}$$

Here the first and second term represent environmental and demographic stochasticity, respectively. Similarly, Eq. (3) splits into two components and the variance σ_V^2 can be written as

$$\lambda^{-2} \sigma_V^2 = \sigma_e^2 + \sigma_d^2/N, \tag{10}$$

where N is the total population size, $N \approx V$,

$$\sigma_e^2 = \sum_{ij} \sum_{kl} \frac{\partial r}{\partial L_{ij}} \frac{\partial r}{\partial L_{kl}} \text{Cov}[E(M_{ij}|\mathbf{z}), E(M_{kl}|\mathbf{z})] \tag{11}$$

and

$$\sigma_d^2/N = \sum_{ij} \sum_{kl} \frac{\partial r}{\partial L_{ij}} \frac{\partial r}{\partial L_{kl}} ECov[M_{ij}, M_{kl}|\mathbf{z}]. \tag{12}$$

The expected yearly change in $\ln V$ is reduced by the demographic stochasticity to

$$E(\ln V_{t+1} - \ln V_t) = r - \frac{1}{2} \sigma_e^2 - \frac{1}{2N_t} \sigma_d^2 = s - \frac{1}{2N_t} \sigma_d^2. \tag{13}$$

Engen et al. (2005) demonstrated by stochastic simulations that the diffusion approximation for N_t , using Eqs. (13) and (10) for the infinitesimal mean and variance, was accurate for small or moderate fluctuations in the growth rate. For more details on the demographic variance and how to estimate it from data see Engen et al. (2005) and Appendix C.

5. Estimation of environmental variance

In populations without age structure the environmental variance can be estimated directly from annual fluctuations in the log population size (Sæther et al., 1998; Lande et al., 2003). In age-structured populations we have seen that these fluctuations also are affected by the process X_t generated by stochastic fluctuations in age structure around the stable age distribution \mathbf{u} . Consequently, in large populations where demographic stochasticity can be

neglected, the variance of $\ln N_{t+1} - \ln N_t$ may be substantially larger or smaller than σ_e^2 , depending on whether environmental stochasticity primarily affects fecundity (and first-year survival) or adult survival, as illustrated below. Even with small or moderate age-structure fluctuations this variance may produce a very strongly biased estimate of the environmental variance indicating that simple methods for estimating key parameters for populations without age structure are quite inappropriate as a basis for evaluating the dynamics of age-structured populations.

If the population is fully censused with correct determination of the age or developmental stage of each individual, we can calculate the reproductive value each year by estimating the L_{ij} by mean values. Since this process behaves exactly as a process without age structure that has environmental and demographic variances σ_e^2 and σ_d^2 , the methods for such populations (Lande et al., 2003) are immediately applicable for the reproductive values. Consider first a large population so that demographic stochasticity can be neglected. Converting an observed multivariate time series of age structures, $\mathbf{n}_0, \mathbf{n}_1, \dots, \mathbf{n}_\kappa$ to a univariate series of total reproductive values, $V_t = \mathbf{v} \mathbf{n}_t$, it follows from Eq. (4b) that the estimate is

$$\hat{\sigma}_e^2 = \frac{1}{\kappa - 1} \sum_{t=0}^{\kappa-1} (\ln V_{t+1} - \ln V_t - \hat{s})^2, \tag{14}$$

where the long-run growth rate is estimated as $\hat{s} = (\ln V_\kappa - \ln V_0)/\kappa$.

When the population is not large, so that demographic stochasticity has to be taken into account, we first estimate σ_d^2 from data on individual survival and reproduction by simple sums of squares as described by Engen et al. (2005). From Eq. (13) it follows that the long-run growth rate for large populations, $s = r - \sigma_e^2/2$, can be estimated as

$$\hat{s} = (\ln V_\kappa - \ln V_0)/\kappa + \frac{1}{2\tilde{N}} \hat{\sigma}_d^2, \tag{15}$$

where \tilde{N} is the harmonic mean of the population sizes for the observed time series.

Similarly, the environmental variance can be estimated by

$$\hat{\sigma}_e^2 = \frac{1}{\kappa - 1} \sum_{t=0}^{\kappa-1} \left(\ln V_{t+1} - \ln V_t - \hat{s} + \frac{1}{2N_t} \hat{\sigma}_d^2 \right)^2 - \hat{\sigma}_d^2/\tilde{N}. \tag{16}$$

Alternatively, the distribution of the differences $\ln V_{t+1} - \ln V_t$ can be approximated by the normal distribution with mean $s - \sigma_d^2/(2N_t)$ and variance $\sigma_e^2 + \sigma_d^2/N_t$ and the likelihood function can be maximized numerically using the estimate of σ_d^2 obtained from individual data. For both methods, uncertainties can be evaluated by bootstrapping, resampling the differences $\ln V_{t+1} - \ln V_t$ with replacement.

If a complete census is not available, but only annual estimates of the population size and age or stage structure,

we can still use the same approach based on estimated reproductive values considering the process as one without age-structure but with sampling errors. The sampling errors can then be handled using Kalman filtering or Markov Chain Monte Carlo methods (DeValpine and Hastings, 2002; Williams et al., 2003).

Holmes (2001) proposed a technique for estimating the environmental variance in the absence of demographic stochasticity from a time series on a density-independent age-structured population with poor or corrupted data (see also Holmes and Fagan, 2002). This is based on estimates of the variance of differences in log population size for a given time increment, τ . For large values of τ the variance of $\ln N_{t+\tau} - \ln N_t$ is asymptotically proportional to τ in the sense that $\tau^{-1} \text{Var}[\ln N_{t+\tau} - \ln N_t] \approx \sigma_e^2$. For example, if $\ln \hat{N}_t$ is an estimate of $\ln N_t$ with constant sampling variance, say c , then $\tau^{-1} \text{Var}[\ln \hat{N}_{t+\tau} - \ln \hat{N}_t] \approx \sigma_e^2 + 2c/\tau$. Hence, plotting estimates of this quantity against τ the environmental variance can be estimated from the asymptote of this curve. Using our decomposition Appendix B shows how to calculate to first order the expected form of this curve to deal with fluctuating age structure caused by environmental stochasticity, rather than uncertainty in estimated population size.

Numerical examples for a simple life history with two stages illustrate that age-structure fluctuations may create a large bias in estimates of the environmental variance. Fig. 1 depicts simulated sample paths (or population trajectories) for the total population size, N , and the corresponding reproductive value, V , with environmental stochasticity either in fecundity (including first-year survival) or adult survival rate. With stochastic fecundity the total population size shows pronounced short-term oscillations, with changes in N tending to exceed those in V . In contrast, with stochastic adult survival the population trajectory fluctuates more smoothly with some tendency to lag behind changes in reproductive value. Fig. 2 shows that environmental stochasticity in fecundity produces an overestimate of σ_e^2 , whereas environmental stochasticity in adult survival produces an underestimate of σ_e^2 . These biases in estimation of the environmental variance may be fairly large unless the time increment exceeds a few generations.

6. An example: Bighorn Sheep

We illustrate our approach by estimating the parameters describing the growth of a population of Bighorn Sheep inhabiting Ram Mountain (52°N, 115°W), Alberta, Canada. Although this population has been intensively monitored since 1971, we only analyzed data from 1981 to 1992 during a period of exponential growth following a time (1972–1980) when individuals were removed for transplantation to other areas (Jorgenson et al., 1993; Festa-Bianchet et al., 1998) and before the population stabilized and subsequently was subject to intensive cougar *Puma concolor* predation (Festa-Bianchet et al., 2006). Our analysis focused only on ewes and their female offspring

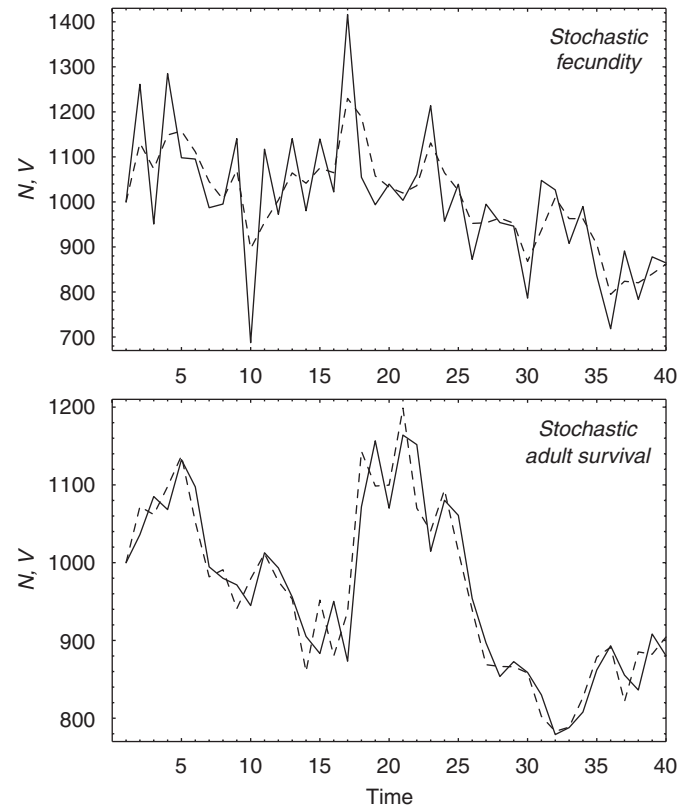


Fig. 1. Simulations of total population size, N (solid lines), and reproductive value, V (dashed lines), for a density-independent population with a simple life history having two stages: juveniles aged 1 year and adults aged 2 years or more. Annual juvenile survival rate is 0.25. Adult annual survival rate, p , has mean 0.5, and adult annual fecundity times first year survival, b (daughters per mother per year), has mean 2, so that in the average environment $\lambda = 1$. Top panel: environmental stochasticity in fecundity times first year survival only, $\sigma_b^2 = 0.25$, $\sigma_p^2 = 0$. Bottom panel: environmental stochasticity in adult survival only, $\sigma_b^2 = 0$, $\sigma_p^2 = 0.01$.

aged at least one year. The nearly exponential increase of the population after the cessation of removals, shown in Fig. 3, established that during this period the population dynamics were density independent, with some stochastic fluctuations. The population was censused just after lambing in June. All adult ewes were marked and resighting probability exceeded 99% (Festa-Bianchet et al., 2003). The age of all individuals was known because they were captured in a corral baited with salt before they were 4 years old, when age can be accurately determined by counting horn annuli (Festa-Bianchet et al., 1998).

The estimate of the demographic variance of the Bighorn Sheep was $\hat{\sigma}_d^2 = 0.112$. Such small demographic variance is typical for species with similar life histories having high adult survival and litters composed of a single offspring (Sæther et al., 2004).

Annual fluctuations in the total reproductive value, V_t , closely tracked those in the size of the breeding population, N_t (Fig. 3), indicating that fluctuations in the age structure do not have a large effect on the parameter estimates for this population. Estimates of the long-run growth rate and

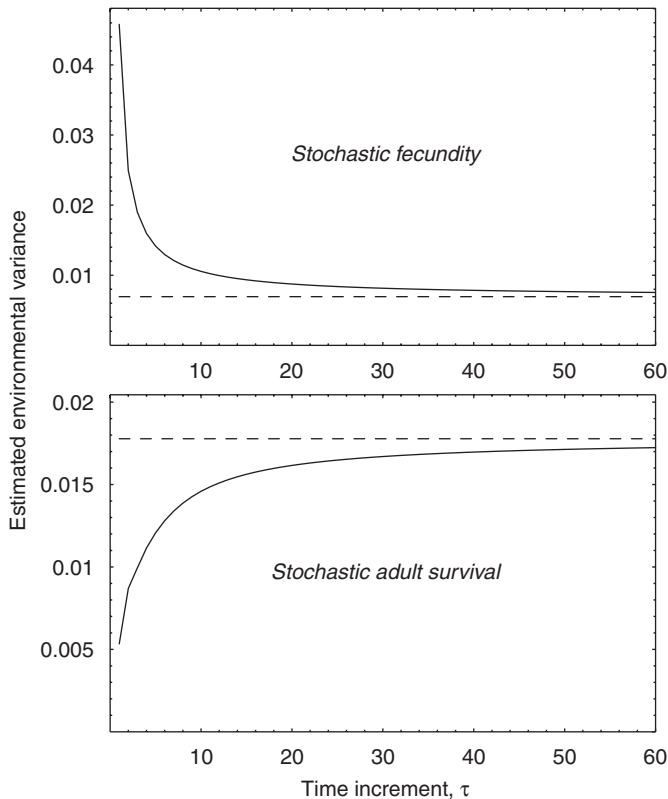


Fig. 2. Bias in estimating the environmental variance in a density-independent population. Results are illustrated for the same life history as in Fig. 1. *Top panel:* environmental stochasticity in fecundity times first year survival only, $\sigma_b^2 = 0.25, \sigma_p^2 = 0$. *Bottom panel:* environmental stochasticity in adult survival only, $\sigma_b^2 = 0, \sigma_p^2 = 0.01$. *Solid lines* give the expected estimate of the environmental variance as a function of the time increment, τ , using the method of Holmes (2001). *Dashed horizontal lines* indicate the true value of the environmental variance, σ_e^2 .

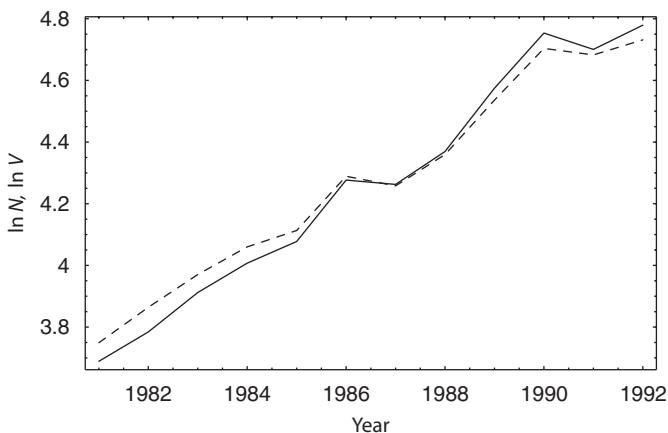


Fig. 3. Annual variation in the natural logarithms of number of females, N_t (solid line), and total reproductive value, V_t (dashed line), for the Bighorn Sheep population.

environmental variance using the simple least-squares formulas (Eqs. (15), (16)), $\hat{s} = 0.088 \pm 0.021$ and $\hat{\sigma}_e^2 = 0.0036 \pm 0.0016$, were very close to those obtained from maximum likelihood, $\hat{s} = 0.088 \pm 0.021$ and $\hat{\sigma}_e^2 = 0.0037 \pm 0.0015$.

7. Discussion

From deterministic models of a density-independent age-structured population it is known that the *per capita* growth rate of the population asymptotically approaches a constant while the age distribution approaches a stable form. Despite departure of the population from the stable age distribution, the total reproductive value always increases at the rate λ (Fisher, 1958; Charlesworth, 1994; Caswell, 1989, 2001). Extending this result to a stochastic environment, we derived Tuljapurkar's approximation to the long-run growth rate of $\ln N$ directly from the expected rate of increase of reproductive value (Eqs. (4a), (4b)).

We also decomposed fluctuations in the log of total population size into the log of reproductive value plus a residual term, $\ln N \approx \ln V + X$. The residual term, X , is continually perturbed away from its mean value of zero by transient fluctuations in age structure driven by environmental stochasticity; however, it is not independent of the reproductive value.

Our analysis showed that fluctuating age-structure can strongly bias estimates of the environmental variance obtained by applying standard methods of time series analysis that ignore age structure (e.g. Turchin, 2003). Even the method of Holmes (2001) and Holmes and Fagan (2002), is subject to this bias, despite being designed to reduce bias due to sampling errors by computing variances of changes in log population size over time increments longer than 1 year. Analysis of a simple life history showed that estimates of environmental variance can be strongly biased either upwards or downwards, depending on whether environmental stochasticity occurs predominantly in adult annual survival or in fecundity and early survival, unless the time increment used in the analysis is at least several generations (Fig. 2). Because most population time series are only a few decades long, this severely limits the applicability of previous methods of estimating the environmental variance for species with generation times longer than a few years.

We showed that bias in estimates of environmental variance can be avoided by analyzing the time series of reproductive values calculated from time series observations on age or stage structure (Eq. (14)). In contrast to the dynamics of total population size, which has multiple time lags depending on the life history (Lotka, 1956; Charlesworth, 1994; Lande et al., 2002a,b), in the absence of environmental autocorrelation the dynamics of reproductive value is a Markovian process (depending only on its current state). This facilitates unbiased estimation of the environmental variance.

Application of our method to estimate the environmental variance requires time series observations of population age or stage structure in order to calculate a univariate time series of reproductive values. This data requirement is much more stringent than for the method of Holmes (2001) which needs only univariate observations on adult or total population numbers through time. Both methods assume no density

dependence. Because density regulation appears to be quite common (Lande et al., 2002a,b; Sæther et al., 2005) applications of such models should be justified ecologically and statistically. On one hand, transient age-structure oscillations, as in the top panel of Fig. 1, could easily be mistaken for density-dependence in a purely univariate analysis of population size. On the other hand, stochastic fluctuations around a gradually declining carrying capacity could appear as a density-independent population decline (Lande et al., 2003, p. 106).

Our model of fluctuations in the vital rates assumes no temporal environmental autocorrelation. Theoretical analysis has shown that environmental autocorrelation can greatly influence population dynamics and extinction risk (Tuljapurkar, 1982; Caswell, 1989, 2001; Ripa and Lundberg, 1996). However, our discrete-time model is primarily intended to apply to species with synchronized annual reproduction, as for many terrestrial vertebrates and plants. Apart from seasonal cycles, weather data in continental areas is not appreciably autocorrelated on time scales longer than 1 year (Namias, 1978), suggesting that for such species environmental autocorrelation is negligible. The short duration of most population time series limits the statistical power to detect temporal autocorrelation in vital rates unless this is rather strong. Analysis of relatively long population time series for several bird species, spanning 30 or more years, failed to detect significant temporal environmental autocorrelation (Lande et al., 2003, pp. 20–23).

We analyzed a population of Bighorn Sheep after the cessation of removal of individuals for restocking other areas. The nearly exponential increase of the population from relatively small numbers over a 12 year period, with some stochastic fluctuations, indicates that during this interval the population growth was density-independent. Because the initial population size was small, we first estimated the demographic variance, σ_d^2 , using data on individual survival of ewes and their production of female offspring surviving to age one (Engen et al., 2005). Using the life table for the pooled data during this period to estimate the average projection matrix, we calculated the reproductive value vector and employed this to convert the time series of population age structure to a univariate time series of total reproductive value. Finally, the least-squares estimators (Eqs. (15) and (16)) were used to obtain the long-run growth rate, s , and the environmental variance, σ_e^2 . Both estimates were statistically significantly different from zero. Estimates from the simple least-squares formulas were very close to those based on maximum likelihood assuming that annual changes in log reproductive values are normally distributed. This justifies the application of the simple least-squares estimators.

Acknowledgments

We thank Tim Coulson for comments on manuscript. This work was partially supported by grants from the

Norwegian Research Council (Strategic University Program in Conservation Biology) to B-ES and SE, and from the US National Science Foundation and the Miller Institute for Basic Research in Science, University of California, Berkeley to RL. A grant from the Natural Sciences and Engineering Research Council of Canada to CF-B supported study of Bighorn Sheep.

Appendix A

A.1. Age-structure fluctuations and variance of population size

In a density-independent population the basic dynamics of the population vector, $\mathbf{n}_{t+1} = (\mathbf{L} + \varepsilon_t)\mathbf{n}_t$, can be linearized by substituting $\mathbf{n}_t = V_t(\mathbf{u} + \mathbf{x}_t)$ and neglecting second-order terms by assuming that the noise ε_t and the deviation from the stable age distribution \mathbf{x}_t are both small,

$$\mathbf{n}_{t+1} = \mathbf{L}\mathbf{n}_t + V_t\varepsilon_t\mathbf{u}.$$

Premultiplying both sides by \mathbf{v} gives text Eq. (2). Premultiplying both sides instead by $V_t^{-1}(\mathbf{I} - \mathbf{u}\mathbf{v})$ using the definition of \mathbf{x}_t in Eq. (6) produces

$$\frac{V_{t+1}}{V_t}\mathbf{x}_{t+1} = \mathbf{L}\mathbf{x}_t + (\mathbf{I} - \mathbf{u}\mathbf{v})\varepsilon_t\mathbf{u}$$

and using text Eq. (2) then shows that to first order

$$\mathbf{x}_{t+1} = \lambda^{-1}\mathbf{L}\mathbf{x}_t + \lambda^{-1}(\mathbf{I} - \mathbf{u}\mathbf{v})\varepsilon_t\mathbf{u},$$

where \mathbf{I} is the identity matrix.

The noise term is identical to that in \mathbf{n}_t , after scaling by λ^{-1} and filtering to remove the component in the direction of the reproductive value vector, \mathbf{v} . Because this component of the noise has been eliminated, it can also be removed from the projection matrix for the process \mathbf{x}_t , replacing \mathbf{L} by $(\mathbf{I} - \mathbf{u}\mathbf{v})\mathbf{L} = \mathbf{L} - \lambda\mathbf{u}\mathbf{v}$. From this argument, and more directly from the definition of $\mathbf{x}_t = \mathbf{n}_t/V_t - \mathbf{u}$ which implies that $\mathbf{v}\mathbf{x}_t = 0$, the dynamics of the residual variation around the stable age distribution can be written as

$$\mathbf{x}_{t+1} = \mathbf{A}\mathbf{x}_t + \lambda^{-1}(\mathbf{I} - \mathbf{u}\mathbf{v})\varepsilon_t\mathbf{u},$$

where $\mathbf{A} = \lambda^{-1}\mathbf{L} - \mathbf{u}\mathbf{v}$.

The expected projection matrix \mathbf{L} can be written in “spectral form” as a sum of factors like $\lambda_i\mathbf{u}^{(i)}\mathbf{v}^{(i)}$ corresponding to the unique eigenvalues, λ_i , plus other terms corresponding to repeated eigenvalues, with the property that $\mathbf{v}^{(i)}\mathbf{u}^{(j)} = 1$ if $i = j$ and 0 otherwise (Gantmacher, 1959). From the Perron–Frobenius theorem for nonnegative matrices, \mathbf{L} has a unique root of largest modulus, denoted as $\lambda = \lambda_1$, that is real and nonnegative, and the corresponding left and right eigenvectors $\mathbf{v} = \mathbf{v}^{(1)}$ and $\mathbf{u} = \mathbf{u}^{(1)}$ have elements that are real and nonnegative (Gantmacher, 1959; Caswell, 1989, 2001). The eigenvectors of \mathbf{A} are therefore the same as those of \mathbf{L} with corresponding eigenvalues $0, \lambda_2/\lambda, \lambda_3/\lambda, \dots$. This clarifies that increasing powers of \mathbf{A} approach the zero matrix, such that if ε_t is a stationary process then the fluctuations in \mathbf{x}_t approach a

stationary process (cf. Tuljapurkar and Lee, 1997). Solving recursively produces

$$\mathbf{x}_t = \lambda^{-1} \sum_{p=1}^{\infty} \mathbf{A}^{p-1} (\mathbf{I} - \mathbf{u}\mathbf{v}) \boldsymbol{\varepsilon}_{t-p} \mathbf{u}.$$

To derive the moments of the stationary distribution of X_t , first note that $E\mathbf{x}_t = 0$ so $EX_t = 0$. The autocovariance function for X_t , given by $\text{Cov}[X_t, X_{t+\tau}]$, can be obtained from the sum of elements of the matrix $E[\mathbf{x}_t \mathbf{x}'_{t+\tau}]$ where $'$ denotes matrix transposition,

$$E[\mathbf{x}_t \mathbf{x}'_{t+\tau}] = \lambda^{-2} \sum_{p=1}^{\infty} \mathbf{G}_p \mathbf{S} \mathbf{G}'_{p+\tau},$$

where $\mathbf{G}_p = \mathbf{A}^{p-1} (\mathbf{I} - \mathbf{u}\mathbf{v})$ and $\mathbf{S} = E[\boldsymbol{\varepsilon} \mathbf{u} \mathbf{u}' \boldsymbol{\varepsilon}']$. The elements of \mathbf{S} are given by $S_{ij} = \sum_k \sum_l u_k u_l \text{Cov}[M_{ik}, M_{jl}]$. The above expression is useful for numerical computations of $\text{Cov}[X_t, X_{t+\tau}]$.

Another expression for σ_X^2 can be derived from the sum of variances and covariances of all left eigenvectors past the first. Consider the factor $V_t^{(i)} = \mathbf{v}^{(i)} \mathbf{n}_t$ associated with the i th left eigenvector of \mathbf{A} , that is $\mathbf{v}^{(i)} \mathbf{A} = (\lambda_i / \lambda) \mathbf{v}^{(i)}$ for $i = 2, 3, \dots$. Premultiplying Eq. (6) by $\mathbf{v}^{(i)}$ gives the basic dynamics of the linearized deviations

$$V_{t+1}^{(i)} = \lambda^{-1} [\lambda_i V_t^{(i)} + \mathbf{z}^{(i)} \boldsymbol{\varepsilon}_t \mathbf{u}]$$

from which we obtain the dynamics of the covariance, $\phi_{ij}(t) = \text{Cov}[Z^{(i)}(t), Z^{(j)}(t)]$,

$$\phi_{ij}(t+1) = \lambda^{-2} [\lambda_i \lambda_j \phi_{ij}(t) + S^{(ij)}],$$

where $S^{(ij)} = \mathbf{z}^{(i)} \mathbf{S} \mathbf{z}^{(j)}$ giving the equilibrium solution, $\phi_{ij} = \phi_{ij}(\infty)$,

$$\phi_{ij} = \frac{S^{(ij)}}{\lambda^2 - \lambda_i \lambda_j} \quad \text{for } i = 2, 3, \dots$$

The variance in the stationary distribution of X , given by the sum of elements of the matrix in Eq. (7), can be compared with these expressions for components of the variance and covariance along directions $\mathbf{v}^{(i)}$. Substitute the spectral decomposition of the matrix power $\mathbf{A}^p = \sum_{j \geq 2} (\lambda_j / \lambda)^p \mathbf{u}^{(j)} \mathbf{v}^{(j)}$ into Eq. (7), noting that the eigenvectors obey the orthogonality relationships $\mathbf{v}^{(i)} \mathbf{u}^{(j)} = 1$ if $i = j$ and 0 otherwise. Then at the stationary distribution

$$\begin{aligned} E[\mathbf{x}_t \mathbf{x}'_t] &= \lambda^{-2} \sum_{p=0}^{\infty} \sum_{i \geq 2} \sum_{j \geq 2} \left(\frac{\lambda_i \lambda_j}{\lambda^2} \right)^p S^{(ij)} \mathbf{u}^{(i)} \mathbf{u}^{(j)'} \\ &= \sum_{i \geq 2} \sum_{j \geq 2} \frac{S^{(ij)} \mathbf{u}^{(i)} \mathbf{u}^{(j)'}}{\lambda^2 - \lambda_i \lambda_j}. \end{aligned}$$

The elements of this matrix can be summed by premultiplying by a row of ones and postmultiplying by a column of ones, noting that because the right eigenvectors $\mathbf{u}^{(i)}$ are normalized to have their elements sum to unity, $(1, \dots, 1) \mathbf{u}^{(i)} = 1$. Hence the variance of the stationary distribution of X is simply the sum of all stationary variances and covariances of the left eigenvectors of \mathbf{A} past

the first,

$$\sigma_X^2 = \sum_{i \geq 2} \sum_{j \geq 2} \frac{S^{(ij)}}{\lambda^2 - \lambda_i \lambda_j}.$$

Appendix B

B.1. Variance of change in log population size

To find the unconditional variance of $\ln N_{t+\tau} - \ln N_t$ we can without loss of generality choose $t = 0$. From our decomposition of the process we have to the first order

$$\ln N_\tau - \ln N_0 = \ln V_\tau - \ln V_0 + X_\tau - X_0.$$

Using Eqs. (2) and (6) in the main text we can write this as

$$\begin{aligned} \ln N_\tau - \ln N_0 &= s\tau + \lambda^{-1} \sum_{p=1}^{\tau} \mathbf{1} \mathbf{u} \boldsymbol{\varepsilon}_{\tau-p} \mathbf{u} \\ &\quad + \lambda^{-1} \sum_{p=1}^{\infty} \mathbf{1} \mathbf{A}^{p-1} (\mathbf{I} - \mathbf{u}\mathbf{v}) (\boldsymbol{\varepsilon}_{\tau-p} - \boldsymbol{\varepsilon}_{-p}) \mathbf{u}, \end{aligned}$$

where $\mathbf{1}$ is a row vector with elements equal to one. Collecting terms with the same time index we see that $\ln N_\tau - \ln N_0 - s\tau$ is the sum of the components of the vector

$$\boldsymbol{\delta}_\tau = \lambda^{-1} \sum_{p=1}^{\infty} \mathbf{C}_p \boldsymbol{\varepsilon}_{\tau-p} \mathbf{u},$$

where $\mathbf{C}_1 = \mathbf{I}$ and

$$\mathbf{C}_p = \mathbf{A}^{p-1} (\mathbf{I} - \mathbf{u}\mathbf{v}) + \mathbf{u}\mathbf{v} = \mathbf{A}^{p-1} + \mathbf{u}\mathbf{v} \quad \text{for } p = 2, 3, \dots, \tau,$$

$$\mathbf{C}_p = (\mathbf{A}^{p-1} - \mathbf{A}^{p-1-\tau}) (\mathbf{I} - \mathbf{u}\mathbf{v}) \quad \text{for } p = \tau + 1, \tau + 2, \dots$$

Evidently the expectation of $\boldsymbol{\delta}_\tau$ is $\mathbf{0}$ so the covariance matrix for the stationary distribution is

$$E[\boldsymbol{\delta} \boldsymbol{\delta}'] = \lambda^{-2} \sum_{p=1}^{\infty} \mathbf{C}_p \mathbf{S} \mathbf{C}'_p.$$

The variance of $\ln N_{t+\tau} - \ln N_t$ is now the sum of the elements of the above covariance matrix. To investigate the behavior of this variance as τ approaches infinity we consider

$$(\ln N_\tau - \ln N_0 - s\tau) / \sqrt{\tau} = \lambda^{-1} \tau^{-1/2} \sum_{p=1}^{\tau} \mathbf{v} \boldsymbol{\varepsilon}_{\tau-p} \mathbf{u} + \tau^{-1/2} (X_\tau - X_0).$$

Since X_t is stationary the last term tends to zero and the variable $\tau^{-1/2} (\ln N_\tau - \ln N_0)$ has asymptotic variance σ_e^2 .

Appendix C

C.1. Demographic variance

To analyze the component of Eqs. (3) and (9) due to demographic stochasticity, following Engen et al. (2005) we introduce for an individual of age i the variables B_i , the

number of offspring, and J_i , the indicator of annual survival. The non-zero elements M_{ij} of the stochastic projection matrix \mathbf{M} in any given year are the mean fecundities $M_{1j} = \bar{B}_j$ and mean annual survival rates $M_{j+1,j} = \bar{J}_j$ among n_j individuals, conditioned on the environment. We assume that survival and reproduction occur independently among individuals when conditioned on the environment. The only non-zero elements of the age projection matrix are the fecundities in the first row and the survival rates along the subdiagonal, and we assume that the only non-zero covariances between distinct elements are for fecundity and survival at a given age. Defining the parameters $\sigma_{B_i}^2 = E \text{Var}(B_i|\mathbf{z})$, $\sigma_{J_i}^2 = E \text{Var}(J_i|\mathbf{z}) = E[\bar{J}_i(1 - \bar{J}_i)|\mathbf{z}]$ and $\sigma_{B_{j_i}}^2 = E \text{Cov}(B_i, J_i|\mathbf{z})$ we find for example

$$E \text{Cov}(M_{1j}, M_{1j}|\mathbf{z}) = n_j^{-1} \sigma_{B_j}^2.$$

Using similar expressions for the other terms we find that the total contribution to Eq. (3) from demographic stochasticity can be written as

$$\begin{aligned} & \lambda^{-2} \sum_{ijkl} v_i u_j v_k u_l E \text{Cov}[M_{ij}, M_{kl}|\mathbf{z}] \\ &= \lambda^{-2} \sum_{j=1}^k n_j^{-1} u_j^2 [v_1^2 \sigma_{B_j}^2 + v_{j+1}^2 \sigma_{J_j}^2 + 2v_{j+1} v_1 \sigma_{B_{j_j}}^2]. \end{aligned}$$

Now, approximating the age distribution by the stable age distribution we have $n_j \approx N u_j$, showing that the demographic term is approximately σ_d^2/N where σ_d^2 is the demographic variance

$$\sigma_d^2 = \sum_{j=1}^k \lambda^{-2} u_j [v_1^2 \sigma_{B_j}^2 + v_{j+1}^2 \sigma_{J_j}^2 + 2v_{j+1} v_1 \sigma_{B_{j_j}}^2].$$

Since $N \approx V$ this indicates that the process for the logarithm of population size can be approximated by a diffusion with infinitesimal mean $r - \sigma_e^2/2 - \sigma_d^2/(2N)$ and infinitesimal variance $\sigma_e^2 + \sigma_d^2/N$.

References

- Caswell, H., 1978. A general formula for the sensitivity of population growth rate to changes in life history. *Theoret. Popul. Biol.* 14, 215–230.
- Caswell, H., 1989. *Matrix Population Models*. Sinauer, Sunderland, MA, USA.
- Caswell, H., 2001. *Matrix Population Models*, second ed. Sinauer, Sunderland, MA, USA.
- Charlesworth, B., 1994. *Evolution in Age-Structured Populations*, second ed. Cambridge University Press, Cambridge, UK.
- Clutton-Brock, T.H., Coulson, T., 2002. Comparative ungulate dynamics: the devil is in the detail. *Phil. Trans. R. Soc. London B* 357, 1285–1298.
- Cohen, J., 1977. Ergodicity of age structure in populations with Markovian vital rates, III: finite-state moments and growth rate; an illustration. *Adv. Appl. Probab.* 9, 462–475.
- Coulson, T., Catchpole, E.A., Albon, S.D., Morgan, B.J.T., Pemberton, J.M., Clutton-Brock, T.H., Crawley, M.J., Grenfell, B.J., 2001. Age, sex, density, winter weather, and population crashes in Soay sheep. *Science* 292, 1528–1531.
- Dennis, B., Munholland, P.L., Scott, J.M., 1991. Estimation of growth and extinction parameters for endangered species. *Ecol. Monogr.* 61, 115–143.
- DeValpine, P., Hastings, A., 2002. Fitting population models incorporating process noise and observation error. *Ecol. Monogr.* 72, 57–76.
- Engen, S., Lande, R., Sæther, B.-E., Weimerskirch, H., 2005. Extinction in relation to demographic and environmental stochasticity in age-structured models. *Math. Biosci.* 195, 210–227.
- Festa-Bianchet, M., Gaillard, J.-M., Jorgenson, J.T., 1998. Mass- and density-dependent reproductive success and reproductive costs in a capital breeder. *Am. Nat.* 152, 367–379.
- Festa-Bianchet, M., Gaillard, J.-M., Côté, S.D., 2003. Variable age structure and apparent density dependence in survival of adult ungulates. *J. Anim. Ecol.* 72, 640–649.
- Festa-Bianchet, M., Coulson, T., Gaillard, J.-M., Hogg, J.T., Pelletier, F., 2006. Stochastic predation events and population persistence in bighorn sheep. *Proc. R. Soc. London B* 273, 1537–1543.
- Fisher, R.A., 1958. *The Genetical Theory of Natural Selection*, second ed. Dover, New York, USA.
- Gantmacher, F.R., 1959. *The Theory of Matrices*, vols. I, II. Chelsea, New York, USA.
- Holmes, E.E., 2001. Estimating risks in declining populations with poor data. *Proc. Natl Acad. Sci. USA* 98, 5072–5077.
- Holmes, E.E., Fagan, W.F., 2002. Validating population viability analysis for corrupted data sets. *Ecology* 2379–2387.
- Jorgenson, J.T., Festa-Bianchet, M., Wishart, W.D., 1993. Harvesting bighorn ewes: consequences for population size and trophy ram production. *J. Wild. Manage.* 57, 429–435.
- Lande, R., Orzack, S.H., 1988. Extinction dynamics of age-structured populations in a fluctuating environment. *Proc. Natl Acad. Sci. USA* 85, 7418–7421.
- Lande, R., Engen, S., Sæther, B.-E., Filli, F., Matthysen, E., Weimerskirch, H., 2002a. Estimating density dependence from population time series using demographic theory and life history data. *Am. Nat.* 159, 321–337.
- Lande, R., Engen, S., Sæther, B.-E., 2002b. Estimating density dependence in time series of age-structured populations. *Phil. Trans. R. Soc. London B* 357, 1179–1184.
- Lande, R., Engen, S., Sæther, B.-E., 2003. *Stochastic Population Dynamics in Ecology and Conservation*. Oxford University Press, Oxford, UK.
- Lande, R., Engen, S., Sæther, B.-E., Coulson, T., 2006. Estimating density-dependence and environmental stochasticity from time series of population age-structure. *Am. Nat.* 168, 76–87.
- Lotka, A.J., 1956. *Elements of Mathematical Biology*. Dover, New York, USA.
- Morris, W.F., Doak, D.F., 2002. *Quantitative Conservation Biology: Theory and Practice of Population Viability Analysis*. Sinauer, Sunderland, MA, USA.
- Namias, J., 1978. Persistence of U.S. seasonal temperatures up to one year. *Mon. Weather Rev.* 106, 1557–1567.
- Ripa, J., Lundberg, P., 1996. Noise colour and the risk of population extinctions. *Proc. R. Soc. London B* 263, 1751–1753.
- Sæther, B.-E., Engen, S., Islam, A., McCleery, R., Perrins, C., 1998. Environmental stochasticity and extinction risk in a population of a small songbird, the great tit. *Am. Nat.* 151, 441–450.
- Sæther, B.-E., Engen, S., Møller, A.P., Weimerskirch, H., Visser, M.E., Fiedler, W., Matthysen, E., Lambrechts, M.M., Badyaev, A., Becker, P.H., Brommer, J.E., Bukacinski, D., Bukacinska, M., Christensen, H., Dickinson, J., du Feu, C., Gehlbach, F., Heg, D., Hötter, H., Merilä, J., Nielsen, J.T., Rendell, W., Robertson, R.J., Thomson, D.L., Török, J., Van Hecke, P., 2004. Life-history variation predicts the effects of demographic stochasticity on avian population dynamics. *Am. Nat.* 164, 793–802.
- Sæther, B.-E., Lande, R., Engen, S., Lillegård, M., 2005. Generation time and temporal scaling of bird population dynamics. *Nature* 436, 99–102.
- Tuljapurkar, S.D., 1982. Population dynamics in variable environments. II. Correlated environments, sensitivity analysis and dynamics. *Theor. Popul. Biol.* 21, 114–140.

- Tuljapurkar, S., Lee, R., 1997. Demographic uncertainty and the stable equivalent population. *Math. Comput. Modelling* 26, 39–56.
- Turchin, P., 2003. *Complex Population Dynamics: A Theoretical/Empirical Synthesis*. Princeton University Press, Princeton, NJ, USA.
- Williams, C.K., Ives, A.R., Applegate, R.D., 2003. Population dynamics across geographical ranges: time-series analyses of three small game species. *Ecology* 84, 2654–2667.